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Contributions from the Cryptogamic Laboratory of Harvard University. XXVIII.

New or peculiar aquatic fungi. 2. *Gonapodya* Fischer and *Myrioblepharis*, nov. gen.

ROLAND THAXTER.

WITH PLATE XXXI.

GONAPODYA Fischer.

In the preceding note on *Monoblepharis* reference was made to the history of this genus which was erected by A. Fischer¹ to receive the single species formerly described by Reinsch² as *Saprolegnia siliquaeformis*. The form was subsequently referred by Cornu³ to his *Monoblepharis prolifera*⁴ but since this name had not been associated with any description or recognizable figure and since its relation to *Monoblepharis* must remain in doubt until more definite information is obtained concerning its sexual reproduction, it would seem proper to retain for the type the specific designation given by Reinsch. It is moreover quite uncertain from published data whether the forms referred to by Cornu and Reinsch are really identical, since a second species described below as *G. polymorpha* is, in this country at least, far more abundant than *G. siliquaeformis*, and may well be the species observed by Cornu. In this author's criticism³ of Reinsch's paper incidental mention is made of the fact that since the publication of his monograph in 1872, he had observed the oospores, which he describes as oval, colorless, contained in oogonia similar to the zoosporangia and resulting from a fertilization of the oosphere by motile antherozoids. Beyond this mere statement, which, to the writer's regret, was overlooked in connection with the previous note on *Monoblepharis*, no further information and no figures of any kind have been published. Although, however, this statement must be accepted as it stands, from so

¹ Rabh. Kryptogamenfl. 14: 382. 1892.

² Pringsheim's Jahrb. f. wiss. Bot. 11: 293. 1876.

³ Bull. Bot. Soc. de France 24: 227. 1877.

⁴ Idem 18: 59. 1871.—Annales d. Sci. Nat. Bot. V. 15: 16. 1872. Van Tieghem, Traite de Botanique 1029. fig. 620, 2.

high an authority, it seems within the bounds of possibility that he may have been misled as to the presence of antherozoids by the extensive variations in size exhibited by the zoospores in certain instances (fig. 14), while the writer must confess that he has himself been several times misled as to the presence of oospores by the encystment of secondary sporangia within the empty primary sporangium, which sometimes occurs under unfavorable conditions. The presence of uniciliate zoospores (which are perhaps not invariably produced in this genus) can hardly be considered very significant in view of the fact that such zoospores are known to occur in other genera, even were it not true that in at least one species of *Monoblepharis* (*M. fasciculata*), if not in all, biciliate zoospores are normally produced.

In other respects the genus bears no resemblance to *Monoblepharis* in appearance or mode of growth, and is well defined through the correlation of successively proliferous sporangia with a habit corresponding essentially to that which distinguishes the order LEPTOMITACEÆ (APODYÆ Fischer), namely the segmentation of its hyphæ through the presence of successive constrictions, each corresponding to a pseudo-septum formed by a deposit of cellulin (?) which nearly closes the passage from one segment to another except for a central perforation through which the protoplasm of adjacent segments may usually be seen to be continuous. This segmentation, however, although as a rule so conspicuous a feature in *G. siliquaeformis*, is sometimes almost wholly absent from, or at least greatly obscured in, the common and very variable species which I have called *G. polymorpha*. The "cellulin rings" in this species are sometimes unassociated with any marked constriction and are sparingly distributed, while in other instances the segmentation is as pronounced as in *G. siliquaeformis*, involving the entire vegetative body when the plant is short in habit, or often confined for the most part, as in fig. 11, to terminal groups of branchlets which are borne on more or less undifferentiated and sparingly pseudo-septate filaments.

The zoosporangia in both species are in general similarly shaped, though much shorter, stouter and smaller in *G. polymorpha*, tapering from a more or less inflated basal portion to the narrow tip which becomes terminally perforate for the emission of the zoospores. The sporangia may be once to several times proliferous and in *G. polymorpha* specimens are

sometimes seen in which the hypha grows on through and beyond the empty sporangium eventually producing new sporangia at its top. The encystment of sporangia formed by proliferation within the empty primary sporangium has already been referred to and has been observed in a number of instances where the fungus was growing under unfavorable conditions surrounded by a mass of bacteria and other plants. The resemblance of such encysted sporangia to oospores is often misleading, but it must be admitted that the walls in such cases cannot be compared in thickness to mature spores of *Rhipidium*.⁵

The zoospores in both species are peculiar in appearance and though sometimes more or less evenly granular, are more commonly sufficiently transparent to show distinctly the large spherical nucleus just in front of which lies a coarsely granular mass characteristically disposed (fig. 10). Each zoospore makes its exit independently and after a short period, during which it undergoes rather rapid amoeboid changes of form, swims away. Zoospores when examined in a partly emptied sporangium may often be seen to creep over its inner surface with an amoeboid motion (fig. 9 below) sometimes disengaging themselves and swimming free in the cavity. In *G. polymorpha* the variations in size exhibited by the zoospores are very remarkable even in the same specimen which may show the extremes represented in fig. 14 produced side by side. The presence of antherozoids in the plant was at first suggested by this great discrepancy, but extended examination shows the occurrence of every degree of variation connecting these extremes.

Reinsch in the paper already mentioned figures⁶ a sporangium in which sporangiola are supposed to have developed from the walls of an empty sporangium, but as such a development is a manifest impossibility, it seems probable that the objects figured are rather zoospores which having been unable to escape have germinated in the position indicated.

In several specimens of *G. polymorpha* oospores such as are represented in fig. 16, have been found associated with the zoosporic form, but in no instance was the material sufficiently good to show the hyphal connections of these spores. They are remarkable for their enormously thickened walls, and

⁵ Cornu l. c.

⁶ l. c., pl. 15. fig. 13.

completely fill the oogonium. In almost every specimen examined the small rounded antheridium was present at the side recalling that of species of *Rhipidium*. It is quite uncertain, however, whether these spores are really connected with the zoosporic form which they accompany.

GONAPODYA SILIQUAEFORMIS (Reinsch). *Plate XXXI, figs. 6-10.*

Saprolegnia siliquaeformis Reinsch l. c.

Gonapodya prolifera Fischer l. c. Schroeter in Engler and Prantl Natürl. Pflanzenfam. 93: 107. 1893.

Hyphæ rather stout, more or less regularly divided into short elliptical to long clavate segments, copiously and successively sub-umbellately branched, the branches diverging in a dense tuft from a common base. Sporangia often once to three times proliferous, long pod shaped, inflated below, the sometimes very elongate distal portion tapering gradually to a blunt apex; borne sessile on the terminal cell of a branch or separated from it by a clearly defined constriction. Zoospores numerous (more than fifty), uniciliate, oval or elliptical with conspicuous nuclei. Oospores (*sec.* Cornu) oval in terminally perforate oogonia like the sporangia. Hyphæ 250-500 μ long, the segments normally about 25 $\times$ 14 μ , but varying greatly. Sporangia, average 130 $\times$ 22 μ , sometimes 200-250 μ long.

On decaying apples in water. Cambridge, Mass., and Kittery Point, Maine.

This species appears to be decidedly rare and has been collected by the writer on two occasions only, growing in dense tufts which formed small pustules on the surface of the substratum above mentioned, and there seems to be no record of its occurrence since it was found by Reinsch in a similar situation. It is distinguished by its very large tapering sporangia, the distal portion of which is sometimes very greatly elongated. Though its hyphæ are commonly rather regularly segmented, forms occur which present great irregularities in this respect, especially through the elongation of terminal branchlets into slender often unsegmented filaments, in a fashion frequently more pronounced than that which is represented in fig. 7. The secondary sporangia are often quite distinct from base to apex within the primary ones, though more commonly the distal portion only is distinct as is represented in fig. 6.

Gonapodya polymorpha, n.sp. *Plate XXXI, figs. 11-16.*—Hyphæ irregularly branched, more or less regularly divided into short oval or irregular segments, the segmented portion arising directly from the substratum or more often confined to tufts of branchlets borne sub-umbellately on the ends of slender elongate hyphæ in which the segmentation is indistinct or obsolete; the segmentation frequently ill-defined or obsolete throughout the whole vegetative body. Sporangia variable in size and form, long-oval, tapering rather abruptly to the blunt tip, terminal and solitary or sometimes several arising from a single segment, once to several times proliferous, the hypha sometimes traversing and growing beyond the empty sporangium. Zoospores very variable in size and number. Hyphæ 200–1000 μ long. Sporangia 20–60 $\times$ 12–30 μ .

On submerged twigs and other vegetable matter. Vicinity of Cambridge, Mass., and Kittery Point, Maine.

This species seems very common and may be obtained from almost any body of still water. Its variability is extraordinary and did not intermediate forms constantly occur one would not hesitate to separate specifically, if not generically, forms in which the segmentation of the hyphæ is most prominent and those in which it is nearly obsolete. Careful search, however, shows the presence of pseudo-septa unassociated with constrictions even in the unsegmented forms. When the segmentation is pronounced it is often even more clearly defined than in *G. siliquaeformis*, as in fig. 15, and in such instances the segmented portions are more often confined to tufts of branchlets borne on slender hyphæ as in figs. 11 and 12.

The oospores represented in fig. 16 have several times been found unassociated with any other zoosporic form, but, as has been already mentioned, a definite connection between the two has not been traced. They occur near the base of the ordinary filaments embedded in the mass of bacteria and foreign matter which is usually associated with this plant. These oospores, which recall those of *Rhipidium* in several respects, are about 54 μ in diameter, the laminated refractive walls 18 μ thick, with the rounded antheridium usually persistent.

The extremes of size exhibited by the zoospores are shown in fig. 14 in two sporangia which were borne side by side on the same filament. The general appearance of the zoospores

also varies greatly, resembling in most cases those of *G. siliquaeformis*, but often densely granular throughout. In some instances the zoospores have seemed to be biciliate.

MYRIOBLEPHARIS.

In examining the material from which the species of *Monoblepharis* already described were derived, I encountered in one instance a singular fungus, remarkable alike for its energetic movements and the unusual character of its zoospores, to which I propose to give the above generic name. In a hasty examination of several preparations the form was at first passed over as an animal, perhaps a rotifer or some similar organism, which had attached itself, either by accident or as a parasite, upon the sporangium of a *Pythium*. Further investigation, however, made it clear that the surprisingly active mass of protoplasm which commonly terminates the plant was concerned in the production of its zoospores, the formation of which was watched from beginning to end in a number of specimens.

The vegetative body of the fungus consists of slender, continuous hyphæ which, arising for the most part singly from the substratum and remaining simple or becoming sparingly branched, bear at their tips the peculiar sporangia represented in the illustrations (figs. 1-4). The primary sporangium is broadly oblong, or elliptic, terminally broadly papillate, and at maturity emits its contents very rapidly in the form of a single mass of protoplasm which at once commences a spasmodic irregularly rotary movement, the violence of which constantly increases. This mass remains adherent to the extremity of the empty sporangium which immediately begins to become proliferous, a new sporangium forming within it very rapidly and at maturity discharging its contents as in the first instance. As a result of this second discharge the first mass is carried up by the second (fig. 2), and each continues its rotating motion, while a third sporangium begins to form rapidly as before within the empty walls of the second. When this third sporangium is beginning to approach maturity, the mass first discharged divides rather rapidly into usually four parts (fig. 3), which undergo very violent movements, whirling around upon one another with great rapidity, but still retaining their position at the summit of the mass discharged from the second sporangium. The third sporan-

gium then empties itself, carrying up the second mass, and, just as this occurs, the rotating bodies above the latter slowly separate from it and from one another, and almost immediately swim off as zoospores. The successive formation of sporangia and the discharge of new masses then continues, the series of sporangia remaining constantly surmounted by two rotating protoplasmic masses, the upper of which breaks up into free swimming zoospores just at the period when a third mass is being discharged. In this way more than a dozen empty sporangia are often superposed as in fig. 2, the series being traversed by the filament which bears them, from the tip of which new sporangia are successively produced. In rarer instances the filament may grow through the sporangium last emptied, and, after having attained a variable length, produces terminally a new series of sporangia as already described. Occasionally, when the successive formation of sporangia has been more than usually rapid, two successively discharged masses may unite with one another, as is shown in fig. 4, where the contents of the sporangium represented in fig. 3 has been discharged and united with the previously discharged mass above it, the two becoming quite indistinguishable from one another.

The successively discharged masses appear to be held in place by, and to go through their peculiar movements within, a perfectly hyaline gelatinous envelope in which each is discharged. The envelope of the first mass does not appear to be broken by the second discharge, and seems to be sufficiently elastic to withstand its pressure until the third discharge takes place, at which moment it is ruptured distally, and allows the escape of the zoospores, which are at this moment fully matured. In this way a series of gelatinous envelopes, corresponding to the series of empty sporangia, is formed, extending from the edges of the mouth of the first sporangium up around the whole series and beyond them to include the two lower masses last discharged. The figures given in the present connection do not show this envelope, being drawn from living material in which its character was not determined. Stained preparations show it very clearly, however, and serve to explain the otherwise inexplicable fixity in position of the three successively discharged masses.

At the time when the zoospores are ready to separate and make their escape, which usually is not less than half an hour

after their discharge as an unsegmented mass, their surface in living material may be seen to be very conspicuously covered with innumerable cilia, as is represented in the illustrations; and, although this has not been made out satisfactorily in living material, stained preparations show that the masses within the gelatinous envelope are similarly ciliate when first discharged. The number of zoospores developed from a single mass is usually four, but is subject to occasional variation, two having been observed in small specimens while in the example represented in fig. 1, the number, originally four, has been increased to five by the division into two of one which was larger than the rest.

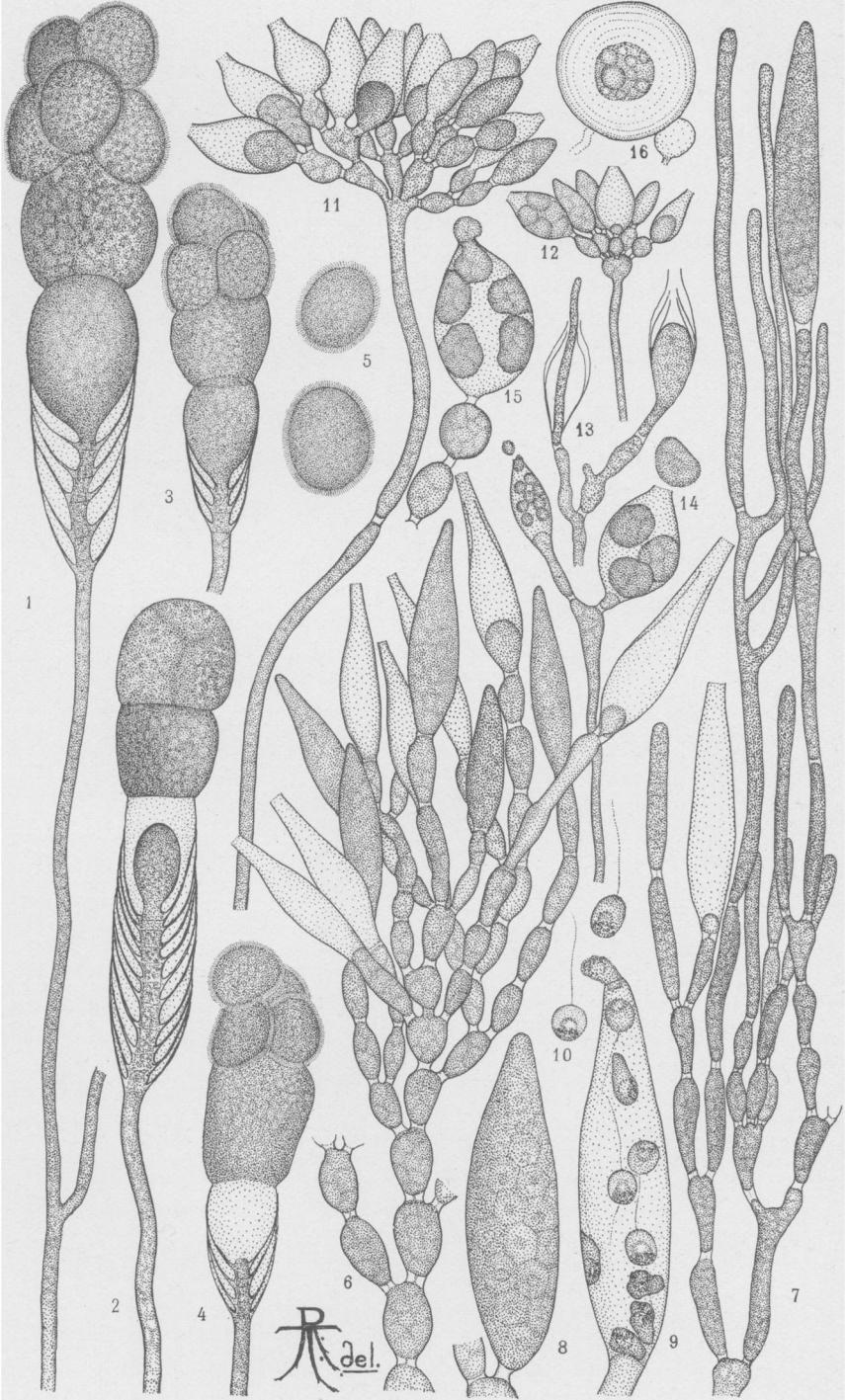
Although resembling some species of *Pythium* both in its slender hyphæ and proliferous sporangia, this genus seems to be clearly distinguished from all other *Phycomycetes* by its multiciliate zoospores and their peculiar process of formation. In fact no other zoospores, except those of *Vaucheria* among the algæ, are known to the writer to possess a similar disposition of cilia. The fate of the zoospores after their escape was not observed, and the sexual reproduction is as yet unknown.

Myrioblepharis, nov. gen. *Plate XXXI, figs. 1-5.*—Hyphæ slender, sparingly branched, bearing terminally zoosporangia becoming many times proliferous and forming an elongate series traversed by the hypha from the successive proliferations of which they arise. Zoospores very large, multiciliate over their whole surface, resulting from the division of the contents of the sporangia which make their exit as a single ciliated mass surrounded by a gelatinous membrane attached to the distal end of the sporangium, the successive envelopes, after rupturing distally, persistent around the series of empty sporangia.

Myrioblepharis paradoxa, nov. sp.—Characters of the genus. The contents of the sporangium dividing into two or four (rarely more) zoospores which are carried upward by the discharged contents of the two sporangia subsequently formed before making their escape from their inclosing envelope. Hyphæ slender, flexuous, seldom more than once or twice branched, about 1^{mm} long, $4-5\mu$ in diameter, sometimes growing through the terminal sporangium of a series and subsequently producing a new series in a similar fashion. Zoospores broadly oval or oblong, $20-30\mu \times 18-20\mu$.

On submerged sticks with *Monoblepharis*, etc. Weston, Mass.

Harvard University.



THAXTER on AQUATIC FUNGI.

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EXPLANATION OF PLATE XXXI.

Myrioblepharis paradoxa Thaxter.

Fig. 1. Branched filament, showing a series of six sporangia, the sixth just ready to empty itself, its papillate tip hidden by the mass above it derived from the fifth sporangium; the contents of the fourth sporangium have divided into five zoospores which escaped immediately after the sixth sporangium discharged its contents.

Fig. 2. A hypha having a series of eleven sporangia, the eleventh half developed, the contents of the ninth borne on that of the tenth, and beginning to segment.

Fig. 3. A condition similar to that represented in fig. 1: the contents of the second sporangium having divided into four zoospores, the fourth sporangium just ready to discharge its contents.

Fig. 4. The same specimen, after the dehiscence of the fourth sporangium, the contents of which have united with those of the third while the zoospores derived from the contents of the second are separating to make their escape.

Fig. 5. Two zoospores showing the extremes of size observed.

Gonapodya siliquæformis (Reinsch) Thaxter.

Fig. 6. Portion of a plant showing elongate segments with two sporangia, one of them empty.

Fig. 7. Portion of a plant showing typical habit; seven of the sporangia are empty, and two of them are once proliferous.

Fig. 8. Sporangium, the contents of which have segmented to form zoospores, its base connected with a segment by a well defined constriction.

Fig. 9. A sporangium, partly emptied, sessile on its segment, the four lower zoospores creeping on the inner surface of the wall.

Fig. 10. Zoospores showing nucleus and anterior granular mass.

Gonapodya polymorpha Thaxter.

Figs. 11-12. Portion of two plants in which the segmented parts are borne sub-umbellately on slender hyphæ.

Fig. 13. Proliferous sporangia, borne on hypha, in which the segmentation is almost obsolete.

Fig. 14. Two sporangia on the same hyphæ, illustrating the extreme variation in the size of zoospores.

Fig. 15. Two segments very clearly distinguished, bearing terminally a sporangium from which the zoospores are escaping.

Fig. 16. Thick walled oospore with antheridium found associated with the zoosporic form, but not definitely connected with it.

*.NOTE.—Figures 1-5, 8-10, 13-15, are drawn with Zeiss obj. D, oc. 4, the remainder with obj. D, oc. 2. All the figures reduced by photo-lithography.